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Volume 17, Number 5 AUGUST, 1942 Serial Number 89

COMPARATIVE PSYCHOLOGY MONOGRAPHS

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Genetic Basis of Spontaneous Activity in the Albino Rat

ELIZABETH GRAVES BRODY
University of Minnesota

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AN EXPLANATION TO SUBSCRIBERS

Readers of this and subsequent issues of this Journal may observe that the pages are somewhat altered in appearance. What is known as the format has been changed. The Journal is now printed on type known as 10-point on a 12-point body, and the type-page is now 29 picas wide and 47 picas long. (A pica is one-sixth of an inch; a point is one-seventy-second of an inch.)

The reason for the change is this: An acute shortage of paper is about to develop. Paper will be increasingly hard to get and it may come to rationing. In the latter case, those who have already made some effort to save paper will doubtless receive more consideration than those who have not.

The new format will permit more words to be printed on fewer pages, without loss of legibility, and without curtailment of the amount of material published. The same amount will be printed on fewer pages—that is all. Issues will be thinner but—to repeat in order to emphasize—just as much material will be published in each volume as has hitherto been published.

In brief, then, the change

1. Tends to forestall a threatened break in the continuity of publication of scientific material, or a curtailment of the amount published;
2. It is a way to assist in the general problem of national defense;
3. It tends to forestall, delay, or minimize a possible rise in price. Labor and materials are going up. Saving paper partly neutralizes the effect.

Finally, some pages in this issue may be printed in the old format. This is merely because these pages happened to be already set in type when the change was determined upon.

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THE GENETIC BASIS OF SPONTANEOUS ACTIVITY IN THE ALBINO RAT[1]

ELIZABETH GRAVES BRODY

University of Minnesota

That genetic constitution is a factor in determining differences in behavior among organisms has been adequately demonstrated. Very few attempts have been made, however, to discover the extent to which differences in behavioral characteristics can be isolated in terms of the genetic laws underlying their inheritance. The purpose of the present investigation has been to determine the extent to which one aspect of behavior in the albino rat, namely, spontaneous activity, can be predicted by means of genetic analysis.

Although studies of activity in the rat have shown that among all animals variations occur which depend upon recurrent organic stimuli, Shirley (3), Slonaker (5), and others have demonstrated that the activity of each animal tends to a relatively constant value during the major part of the life cycle. This indicates that differences in activity level can be attributed to basic physiological mechanisms apart from immediate interoceptive stimuli. Two important physiological factors which have been found to affect activity level are sex and age.

An important step in the analysis of spontaneous activity is the isolation of additional factors which impose restrictions upon the amount of variation exhibited by a given individual. That genetic constitution is in part responsible for the differences in activity found among individuals of the same sex and age is demonstrated by Rundquist's experiment (2) in which strains of active and inactive rats were separated by means of selective breeding.

In the present experiment the two strains initially separated by Rundquist were utilized in a series of cross matings after selective breeding had been in progress for twenty-one generations. The genetic analysis undertaken in the present study is based both upon the results of strain crosses among rats in the F_{21} and F_{22} generations and upon the results obtained during the first twenty-nine generations of selection.

The conditions of this experiment are similar to those described by Rundquist during the separation of the active and inactive strains. The revolving drum was employed for the measurement of activity. Each animal was placed in a cage equipped with a food cup and water bottle. Daily records of activity were taken during a three-week period. A counter attached to each cage recorded the distance traveled in terms of quarter revolutions in either direction.

The number of revolutions made during a fifteen-day period was used as an index of spontaneous activity. Although the rats remained in the cages for twenty-one days, records for only the last fifteen days were used. This procedure was followed since it has been found that a four- or five-day pre-test period is necessary for adaptation (3). That this method provides a reliable measure of activity was demonstrated by Rundquist in an analysis of the consistency of activity for three consecutive five-day periods. His results indicate that errors of measurement are relatively unimportant as a factor in determining differences in activity.

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[1] The writer is indebted to Dr. William T. Heron and Dr. Clarence P. Oliver for helpful suggestions and criticisms.

The animals were placed in activity cages at ages varying from sixty to one hundred days. On the basis of previous studies it is highly improbable that the variation in age in this study had any appreciable effect upon activity. Slonaker (5), Shirley (3), and Richter (1) have conducted extensive experiments on the activity of rats throughout the major part of the life period. Their data agree in showing that young and very old animals are quite inactive but that there is little change in activity level from puberty to the age of one hundred days.

RESULTS

A. Effects of selective breeding on activity[2]

In the early stages of isolating the active and inactive strains mass selection was practiced. Since it was important to obtain as wide a range as possible from which to select, matings were made solely on the basis of individual activity. No attempt was made to keep within a strain in selecting the parents of the next generation. From the F_5 generation on, however, matings were based solely on the extremes within a strain.

The effects of selective breeding are presented for twenty-nine generations of active animals and twenty-five generations of inactive animals. Although animals from both strains remained in good physical condition, the active strain tended to produce somewhat larger litters, had more fertile matings, and was characterized by a shorter period of time elapsing between time of mating and littering. The difference in litter size did not increase progressively with continued selection, but the inactives tended to become less fertile until finally such a small number of litters were produced that the strain could not be continued after the twenty-fifth generation. The relation of these factors to activity will be discussed later.

In figure 1 the mean and standard deviation of activity throughout selection are presented for each generation. Since the females are much more active than the males the results are shown separately for each sex. It will be noted that the parent generation was relatively inactive and that the initial effect of selecting either active or inactive rats for mating was an increase in the activity of the offspring. The inefficacy of initial selection in separating the two strains is apparent when the means and standard deviations of the F_4 generation are compared. However, the selection of inactive animals from this combined distribution resulted in a marked decrease in the activity of the F_5 generation and the strains are clearly differentiated from this point on.

It is evident that the mean activity of the active strain was not increased by further selection. The means of all the generations of active females fluctuate around a value of 207,900 revolutions and the means of the active males fluctuate around a value of 145,500 revolutions. Although the means show no consistent increase with further selection it might be expected that rigorous selective breeding would reduce the variability of individuals within the active strain. However, this has not occurred. It will be noted that the absolute variability in the active strain tends to fluctuate around the same level for all generations among both the males and females. The standard deviations of the active females fluctuate around a mean of 71,210 revolutions and those of the males around a mean of 70,170 revolutions.

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[2] The data for this section were obtained from Rundquist's results on the first twelve generations and thereafter are based on the accumulated records.

Within the inactive strain the mean activity of the females decreased to some extent following the fifth generation and a corresponding decrease in the standard deviations also occurred. Among the successive generations of inactive males the means and standard deviations decreased to only a slight extent after the initial separation.

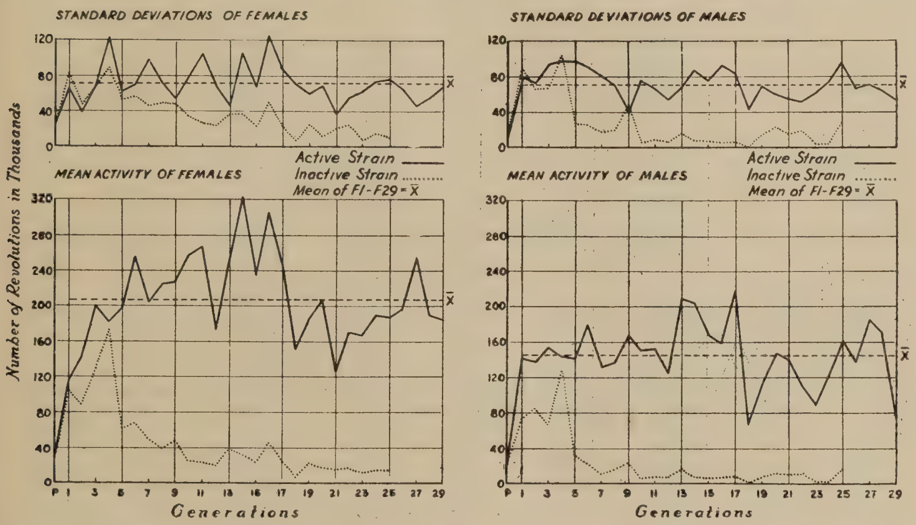


FIG. 1. THE MEANS AND STANDARD DEVIATIONS OF ACTIVITY OF THE ACTIVE AND INACTIVE STRAINS DURING SELECTIVE BREEDING

The sex difference within the active strain will be discussed later, but it is evident that the males and females differ only in mean activity and not in variability. Within the inactive strain, on the other hand, both the means and standard deviations of the females tend to exceed those of the males. However, by the eighteenth generation the means and standard deviations of the females have decreased to approximately the same level as the means and standard deviations of the males.

The coefficients of variability presented in figure 2 also clearly indicate that the heterozygosity within the active strain has not been reduced by means of selection. It will be noted that the level of fluctuation tends to remain the same throughout all generations. The relative variability of the active males is consistently higher than that of the females since the absolute variability was approximately the same for the two sexes whereas the mean of the males was considerably lower.

The relative variability of the inactive strain is much higher than that of the active strain. For the females it fluctuates around a value of 1.00 and among the males it is even higher. The fact that the means and standard deviations tend to have approximately the same value in the case of the females and that the standard deviations exceed the means in the case of the males indicates that the distributions are very skewed. However, it will be noted that the amount of skewness does not tend to increase with continued selection despite the tendency for the mean activity to decrease. As will be pointed out later the number of very active animals is reduced somewhat with progressive selective breeding, but the number of very inactive animals does not increase. The tendency for the relative variability of the inactive strain to remain constant is indicated even more strikingly by the correlations between the means and the standard deviations. For the F_5 to F_{25} generations the correlation was +0.83 for the males and +0.95 for the females. The means, standard deviations, and coefficients of variability which are shown graphically in figures 1 and 2 are presented also in tables 1 and 2 for the active and inactive strains respectively.

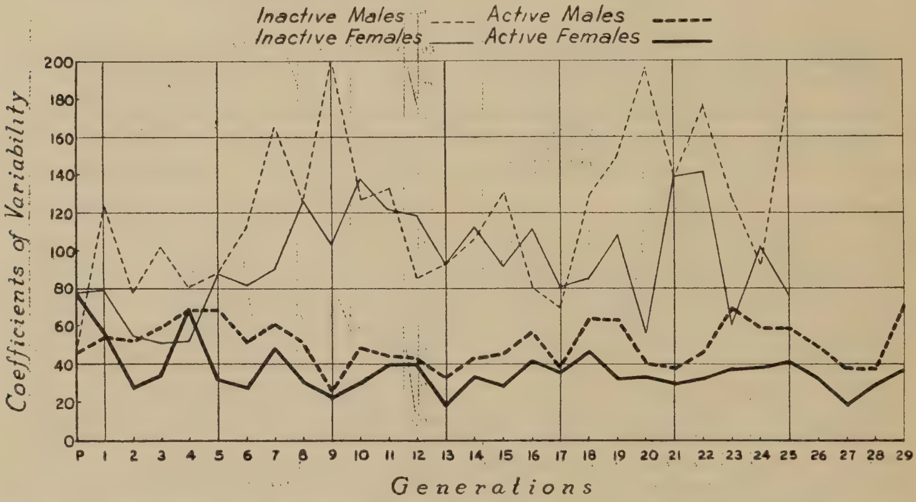


FIG. 2. COEFFICIENTS OF VARIABILITY OF ACTIVE AND INACTIVE MALES AND FEMALES DURING SELECTIVE BREEDING

The cumulative frequency distributions of the activity of active and inactive strain animals throughout selection are shown in figure 3. Each successive five generations have been grouped together in order to indicate more clearly the trends during the first twenty-five generations.

It will be noted that the distributions of activity for both the active and inactive strain are represented as having a zero origin. Although the percentages plotted at zero include all animals that ran less than 1,000 revolutions, the major proportion of these very inactive rats ran less than 500 revolutions during the fifteen-day period. The extremely inactive rats made virtually no movements during the entire period except to obtain food and water. The lower limits of both the active and inactive distributions, therefore, approach an absolute zero.

It has not been possible to eliminate inactive offspring from the active strain by means of selective breeding. The sole effect of selection has been the elimination of active offspring from the matings among inactive animals. That the later generations of active strain rats are no more active than the earlier generations is shown here as well as in the distributions of mean activity. The abrupt transition between the active and inactive strains is clearly shown in the distributions of male activity. The distribution of the first five inactive generations is the only intergrade between the two series of curves. The same is true in general for

TABLE 1

The mean activity and variability of the active strain during selection

GENERATION	ACTIVE FEMALES				ACTIVE MALES			
	N	Mean	Standard deviation	Coefficient of variability	N	Mean	Standard deviation	Coefficient of variability
1	10	115,100	65,430	56.8	17	140,647	78,033	55.5
2	9	141,778	39,264	27.7	10	137,600	71,552	52.0
3	7	200,000	66,716	33.4	7	153,000	91,586	59.8
4	31	180,774	121,618	67.4	24	142,500	95,927	67.5
5	22	198,227	61,047	30.8	19	140,987	95,877	68.0
6	23	255,000	69,218	27.2	30	177,600	89,756	50.5
7	27	204,889	96,767	47.2	28	130,929	79,617	60.5
8	29	234,000	70,204	30.0	29	136,483	69,932	51.2
9	20	237,400	52,778	22.3	32	168,031	40,997	24.4
10	26	256,731	76,500	29.8	26	150,346	74,760	48.5
11	25	267,120	103,625	38.8	26	151,154	66,292	43.9
12	23	172,174	66,449	38.6	26	123,154	52,968	43.0
13	13	253,076	45,842	18.1	22	209,090	67,324	32.2
14	17	322,060	105,285	32.7	29	204,310	87,315	41.8
15	24	233,500	65,858	28.2	29	166,550	74,910	45.0
16	23	305,215	124,955	41.0	26	159,230	90,560	56.8
17	31	249,195	88,490	35.6	25	217,200	82,798	38.2
18	15	150,000	68,995	46.0	14	66,435	42,150	63.3
19	34	184,700	59,400	32.2	31	110,975	69,000	62.1
20	47	207,020	68,600	33.1	37	147,360	59,850	40.6
21	13	125,076	36,720	29.4	14	140,000	53,800	38.4
22	21	169,040	54,000	31.9	19	110,130	50,700	46.0
23	24	165,625	61,750	37.2	28	87,860	60,400	69.0
24	26	189,425	71,500	37.8	29	121,040	71,600	59.2
25	40	187,000	75,400	40.3	43	161,325	94,250	58.5
26	33	195,825	63,750	32.5	25	137,200	67,200	48.9
27	29	255,520	45,600	17.9	33	185,160	69,800	37.7
28	43	189,540	53,400	28.2	44	170,460	63,600	37.4
29	33	183,320	65,800	35.9	47	73,400	52,000	70.9

the females but the variation among the different groups of active generations is more marked than among the males. In addition, the inactive generations show some progressive downward shift.

Since selective breeding was not effective in altering the amount of activity manifested by individuals within the active strain, the distributions of activity among all the generations have been combined into a single distribution in the attempt to ascertain better the nature of this trait. In figure 4 the composite frequency distributions of activity of the active males and females for all generations are presented. As noted previously, the means of the total populations are 207,900 revolutions for the females and 145,500 for the males. However, the standard deviations of the total populations are somewhat higher than the means of the standard deviations of the separate generations. The standard deviation of activity of the population of females is 83,240 revolutions and of the population of males 80,140 revolutions.

TABLE 2

The mean activity and variability of the inactive strain during selection

GENERATION	INACTIVE FEMALES				INACTIVE MALES			
	N	Mean	Standard deviation	Coefficient of variability	N	Mean	Standard deviation	Coefficient of variability
P1	24	28,083	21,772	77.5	24	20,917	9,545	45.6
F1	9	103,889	82,717	79.5	14	71,714	88,969	123.4
2	18	89,500	48,181	53.9	15	83,533	65,180	78.0
3	7	129,000	65,458	50.7	13	65,231	66,404	102.0
4	20	172,700	89,365	51.7	25	128,640	103,528	80.6
5	20	59,850	52,389	87.5	16	31,125	27,217	87.6
6	25	68,080	55,368	81.4	23	22,217	24,728	111.1
7	28	50,286	45,073	89.8	18	10,111	16,673	164.0
8	19	39,474	48,966	125.8	11	15,091	18,790	125.0
9	25	46,280	47,474	102.7	21	22,381	44,625	200.0
10	23	24,478	33,683	137.5	25	3,680	4,670	126.7
11	29	22,621	27,517	121.6	21	6,476	8,501	131.6
12	23	20,391	24,202	118.7	29	6,241	5,296	84.8
13	26	39,615	36,258	91.7	24	15,625	14,296	91.7
14	13	32,692	36,389	111.3	18	6,944	7,372	106.5
15	22	23,638	21,545	90.9	17	4,765	6,216	130.0
16	27	44,260	49,017	110.6	28	5,500	4,411	80.1
17	20	25,500	20,428	80.1	17	7,235	4,994	69.0
18	7	7,280	6,180	84.9	8	726	934	128.2
19	17	22,080	23,760	108.0	28	7,720	11,480	149.3
20	18	18,180	10,140	55.7	17	11,460	22,440	196.5
21	56	14,500	20,100	138.5	48	10,080	13,960	139.0
22	24	17,080	24,100	140.9	14	11,070	19,400	175.6
23	9	10,956	6,640	60.4	14	2,150	2,709	126.8
24	13	12,885	13,050	101.1	9	2,600	2,392	91.7
25	6	13,000	9,940	76.5	9	16,332	29,520	181.8

Both of these distributions of activity closely approximate a normal curve despite the tendency toward a concentration of cases at the inactive extreme. Since the mean of the females differs from zero by only 2.50 sigma units and that of the males by only 1.82 sigma units, 3.44% of the males and 0.62% of the females would be expected to occur outside the possible range. When the numbers of males and females in the lowest class intervals are increased by these corresponding amounts, the actual distributions do not differ significantly from the normal type.

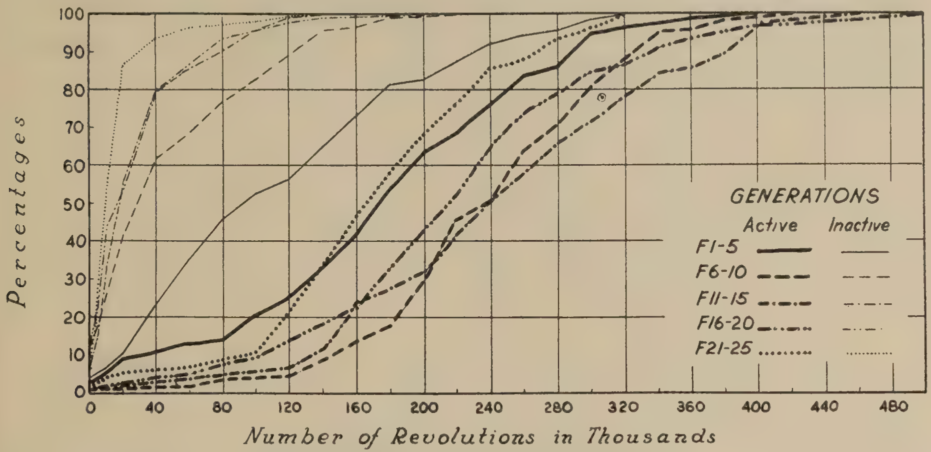


FIG. 3*a*. CUMULATIVE PERCENTAGE FREQUENCY DISTRIBUTIONS OF THE ACTIVITY OF FEMALES IN THE ACTIVE AND INACTIVE STRAIN GROUPED BY SUCCESSIVE FIVE GENERATIONS FROM THE F1 TO THE F25 GENERATION

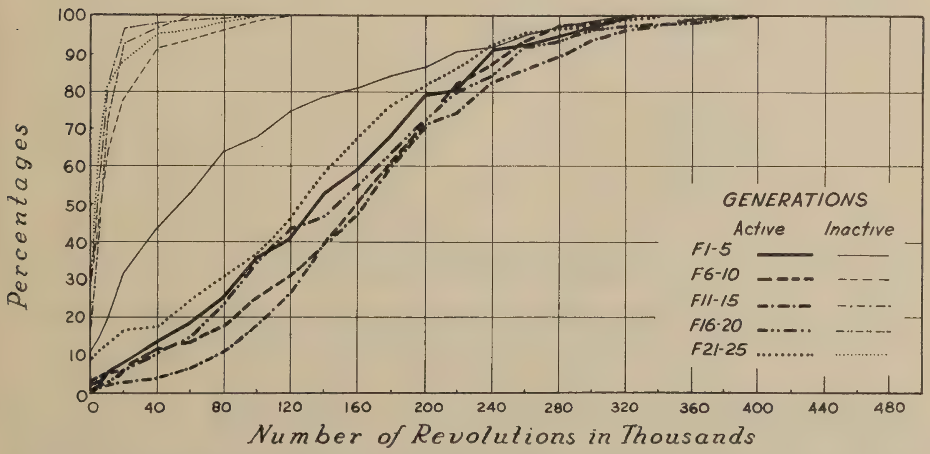
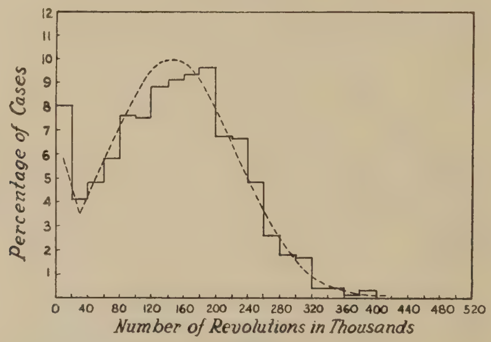


FIG. 3*b*. CUMULATIVE PERCENTAGE FREQUENCY DISTRIBUTIONS OF THE ACTIVITY OF MALES IN THE ACTIVE AND INACTIVE STRAIN GROUPED BY SUCCESSIVE FIVE GENERATIONS FROM THE F1 TO THE F25 GENERATION

In testing the "goodness of fit" the values of X^2 obtained were 15.53 for the males with 14 degrees of freedom, and 20.79 for the females with 18 degrees of freedom. In both cases the probabilities are considerably above the 20% level of significance.[3] This bears out the assumption that the distributions do not differ significantly from the normal probability curve.

The forms of the distributions of activity among the males and females are practically identical which indicates that the factors responsible for individual variation are the same for the two sexes. The distributions differ, therefore, by a constant factor. If the activity of each male were increased by the difference between means, 63,400 revolutions, the two curves would coincide.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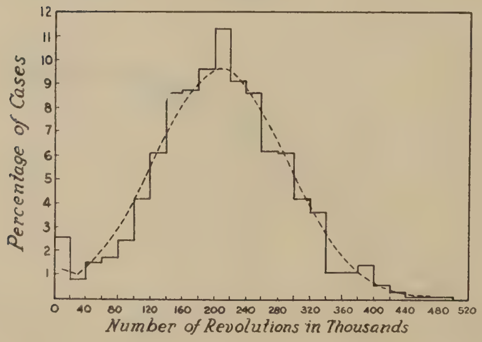
b. FEMALES

Fig. 4. The Distributions of Activity of Males and Females in the F21–F29 Generations of the Active Strain in Terms of Percentages with Superimposed Normal Frequency Curves

The concentration of animals at the inactive extreme indicates that the measuring instrument is unable to distinguish differences among extremely inactive individuals. That increasing the length of the testing period would not alter the position of the distributions is evident since this would increase only the relative activity of each animal.

Although activity among both the males and females is distributed in accordance with the normal curve, the differences among generations cannot be attributed to purely random factors since there is a marked tendency for the means of the active males and females to fluctuate concomitantly. The correlation of +0.60 between the means for the two sexes is highly significant.

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[3] Table IV, page 27. Fisher, R. A. and Yates, F. Statistical Tables for Biological, Agricultural, and Medical Research. 1938.

Whether or not activity within the active strain differs significantly from one generation to the next can best be ascertained by means of an analysis of variance. The total variation in the combined generations is dependent upon both the variation among different generations and the variation within each generation. An analysis of variance permits the independent estimation of variability in terms of these two sources. The results of this analysis are presented in table 3.

For the females the ratio of the mean square "between generations" to the mean square "within generations" is 12.78. For the males the corresponding ratio has a value of 9.54. In both cases the variation between generations is significantly greater than that within generations,[4] that is, the mean activity from one generation to the next differs far more than would be expected on the basis of random sampling. These results indicate that the total variation within the active strain depends to a marked extent upon the effect of a differential environment acting upon the various generations.

TABLE 3

Analysis of variance of the activity of all generations in the active strain

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARES
A. Females			
Between generations	28	1,704,497	60,874.8
Within generations	698	2,325,883	4,764.9
Total	726	5,030,380	
B. Males			
Between generations	28	1,311,341	46,833.6
Within generations	743	3,646,042	4,907.2
Total	771	4,957,383	

An additional analysis was conducted to determine whether there were any significant differences in the extent of variation among individuals from one generation to another. The test of significance of the difference among group variances yielded a X^2 value of 21.77 for the males with 28 degrees of freedom and a X^2 value of 14.53 for the females with 28 degrees of freedom. In each case X^2 has a probability value above the 50% level of significance.[5] Thus it is evident that although the mean activity differs significantly from one generation to the next, the extent of variation among individuals does not differ significantly among successive generations. The latter analysis is further evidence that selective breeding has not been effective since any genetic differences among generations would, of course, affect the variability.

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[4] Table 10.3, page 184–187. SNEDECOR, G. W. Statistical Methods. 1938

[5] Table IV, page 27. FISHER, R. A. AND YATES, F. *Op. cit.*

On the basis of these results it can be concluded that the various generations of active rats do not differ as a result of genetic factors but that environmental differences exercise a marked effect upon the expression of the trait.

The fact that the activity of the females and to a lesser extent of the males within the inactive strain continued to decrease with selection, suggested the possibility that differences in activity arose from the cumulative effects of different gene pairs. It is apparent that if such a hypothesis were true the number of extremely inactive animals should increase coincident with a decrease in the number at the most active end of the distribution.

In figure 5 the percentage of animals that ran less than 1000 revolutions during the fifteen-day period is shown. More males than females were very inactive as might be expected but for neither sex does the proportion increase to any marked extent with continued selection. Furthermore, wide fluctuations from one generation to the next occur. These fluctuations cannot be attributed to errors of random sampling since the males and females tend to vary concomitantly.

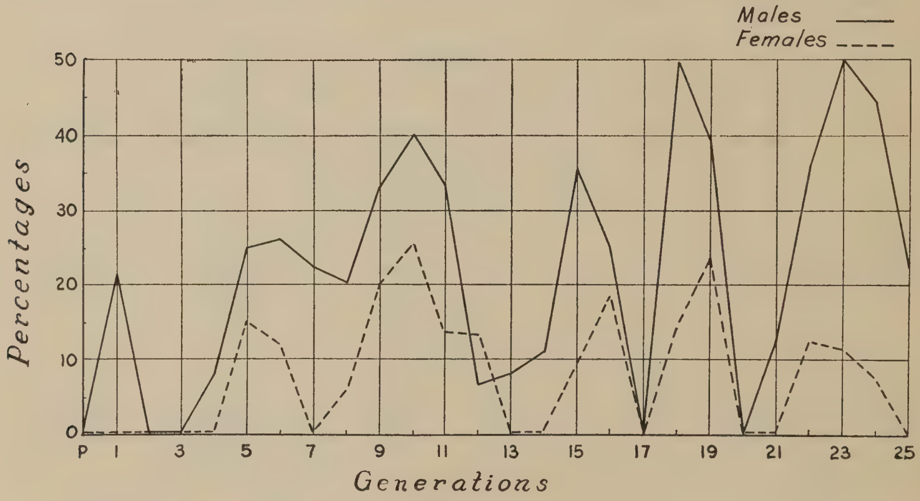

Fig. 5. Percentages of Males and Females in the Inactive Strain that Ran Less than One Thousand Revolutions

In table 4 is presented a comparison of the number of animals below 1000 revolutions from the fifth to the nineteenth generations derived from crosses of: (1) both parents below 1000 revolutions, (2) male parent below 1000 revolutions, and (3) neither parent below 1000 revolutions. (No very inactive females were mated to less inactive males.) The inactive crosses yielded only a slightly larger percentage of very inactive males than did either of the other two crosses. A comparison of all the offspring of very inactive parents with offspring from less inactive parents showed no significant differences in activity whatsoever. This suggests that environmental factors are responsible for the variation. Although there are no significant differences in activity among the crosses, one difference that may be significant is the reduced number of males per litter in the very inactive crosses.

Additional evidence that recessive multiple factors cannot account for inactivity is provided by the coefficients of variability which showed that the amount of skewness tended to remain the same throughout selection.

From the fifth generation on the two strains are clearly differentiated on the basis of the production of active offspring as shown by the fact that in the inactive strain no females exceeded 180,000 revolutions and no males exceeded 140,000 revolutions. Further selection had no effect upon reducing the proportion of inactive animals within the active strain. The proportion of very inactive animals within the inactive strain did not increase although some additional decrease in the number of active animals did occur.

TABLE 4

Analysis of several classes of matings within the inactive strain

	BOTH PARENTS VERY INACTIVE	MALE PARENT VERY INACTIVE	NEITHER PARENT VERY INACTIVE
Number of litters	13	31	49
Number of very inactive males	47	101	153
Number of very inactive females	61	105	159
Per cent very inactive males	25.6	24.8	23.6
Per cent very inactive females	13.1	11.4	10.7
Average males per litter	2.76	3.26	3.12
Average females per litter	3.59	3.39	3.24
Sex ratio	0.77	0.96	0.96

If a large number of genes differentiate the two strains, the distributions of activity of the inactive animals should gradually have changed in form with selection until a limiting J-shaped distribution was finally reached. On the contrary, the transition from the active distribution to the inactive is abrupt with no very active animals resulting from inactive matings following the F_5 generation. This suggests that differences between the strains may be attributed to only a small number of genes. Additional evidence as to the genetic factors differentiating the two strains will be discussed when the results of the cross-matings are presented.

It has already been mentioned that the inactive strain could not be continued beyond the F_{25} generation because no offspring were obtained from the majority of matings. No absolute basis of comparison between the two strains in fertility is possible since, in general, if by the end of six weeks to two months the females had not littered the matings were discontinued. However, during the last few generations the inactive females were so infertile that they were mated and remated several times for as long a period as six months.

In table 5 the percentages of females that cast litters within the two strains are presented for each successive five generations throughout the first twenty-five generations of selection. The percentages do not exhibit consistent trends, but it will be noted that whereas both the actives and inactives decreased in fertility during the F_{16}–F_{20} generations, the active strain increased in the last few generations while the inactive strain continued to drop.

The average number of males and females per litter and the sex ratios obtained in each generation are presented in table 6. A comparison between the two strains in litter size is shown graphically in figure 6. A simple three point smoothing was applied to the actual litter size values to eliminate minor fluctuations and thus more clearly to express the general trends. It will be noted that the curves for the active and inactive females are very much alike. The initial effect of selection was an increase in the number of females per litter followed by a gradual decrease up to about the thirteenth generation. Despite the similarities among the females the number of males in the two strains differs markedly. The number of inactive males tends to increase somewhat initially corresponding with an increase in the number of females but a marked decrease occurs from the fifth to the sixth generation followed by a smaller decrease up to the eighth generation. On the other hand, the number of active males increases from the third generation up to the eighth generation at which point the average number of inactive males per litter is only one-half the number of active males. The combined litter sizes from the sixteenth to the twenty-fifth generation show no statistically significant differences either between sexes or between strains. Obviously the striking difference between males in the earlier generations cannot be a direct function of the genes which differentiate the two strains or the difference would persist throughout all the generations.

TABLE 5

The fertility of matings within the active and inactive strain during selection

GENERATIONS	PER CENT FERTILE ACTIVES	PER CENT FERTILE INACTIVES
1–5	81	84
6–10	86	76
11–15	81	85
16–20	59	68
21–25	78	37

Although the active and inactive strains do not differ significantly with respect to the average number of females per litter, the mean activity of the females within the inactive strain is significantly related to the number per litter. Not only does the mean activity tend to decrease concomitantly with the decrease in litter size but the trend fluctuations also occur together.

Since mean activity and litter size both exhibit a certain amount of irregular fluctuation, correlation coefficients were calculated from the smoothed data to obtain a more accurate representation of the similarity in trend. The correlation between activity and the number of females per litter within the inactive strain from the fifth to the twenty-fifth generation was +0.81 which is even higher than the correlation of +0.77 between the number of females per litter in the active and inactive strains.

The similarity in pattern between the active and inactive females suggests that the decline in litter size results from a general decrease in heterozygosity in both strains and that the concomitant fluctuations result from environmental factors. The data also suggest that the decrease in activity within the inactive strain following strain separation can be attributed to a decrease in heterozygosity.

TABLE 6

The litter sizes and sex ratios of the active and inactive strains during selective breeding

	ACTIVE STRAIN				INACTIVE STRAIN			
	No. of litters	Average no. of males	Average no. of females	Sex ratio	No. of litters	Average no. of males	Average no. of females	Sex ratio
F1	4	4.25	2.50	1.70	4	3.50	2.25	1.56
2	4	2.50	2.25	1.11	5	3.00	3.60	0.83
3	3	2.33	2.33	1.00	3	4.25	2.33	1.86
4	6	4.00	5.17	0.77	5	5.00	4.00	1.25
5	5	3.60	4.40	0.82	5	3.20	4.00	0.80
6	6	5.00	3.83	1.30	6	3.83	4.17	0.92
7	7	4.00	3.86	1.04	8	2.25	3.50	0.64
8	6	4.83	4.83	1.00	5	2.00	3.60	0.56
9	5	6.40	4.00	1.60	7	3.00	3.57	0.84
10	7	3.71	3.71	1.00	7	3.57	3.29	1.09
11	7	3.71	3.57	1.04	10	2.10	2.90	0.72
12	6	4.33	3.83	1.13	8	3.63	2.88	1.26
13	5	4.20	2.60	1.62	9	2.67	3.00	0.89
14	7	4.29	2.43	1.76	5	3.60	2.60	1.38
15	9	3.56	3.00	1.19	6	2.83	3.67	0.77
16	6	4.33	3.83	1.13	7	4.00	3.86	1.04
17	10	2.50	3.10	0.81	5	3.40	4.00	0.85
18	5	3.60	3.40	1.06	4	3.50	1.75	2.00
19	12	3.58	3.25	1.10	10	3.50	3.40	1.03
20	18	3.44	3.05	1.14	13	2.85	3.39	0.84
21	7	3.14	3.28	0.96	18	3.39	3.61	0.94
22	5	3.80	4.40	0.85	7	2.29	3.43	0.67
23	11	3.00	2.55	1.18	6	3.16	1.67	1.89
24	9	3.78	3.00	1.26	4	3.25	3.25	1.00
25	11	4.82	4.09	1.18	2	4.50	3.50	1.29

The correlation found between the number of males per litter in the two strains was −0.13, and the correlation between male activity and the number per litter within the inactive strain was +0.46. Among the inactive strain males the decrease in both mean activity and number per litter was sudden rather than gradual in contrast to the trend shown by the females. However, the largest decrease in the number of males per litter occurred in the generation immediately following strain separation rather than simultaneously. It is probable that the difference in the number of males, although not directly determined by the genetic difference between strains, is indirectly affected through certain modifying factors. As noted previously, the number of males tends to be lowered to a considerable extent by crosses between two very inactive parents.

The preceding data on the relation of litter size to activity must be regarded as suggestive rather than conclusive evidence, but certainly it would appear that although the genetic difference between strains does not determine differences in litter size, some of the variations in litter size and activity are codetermined.

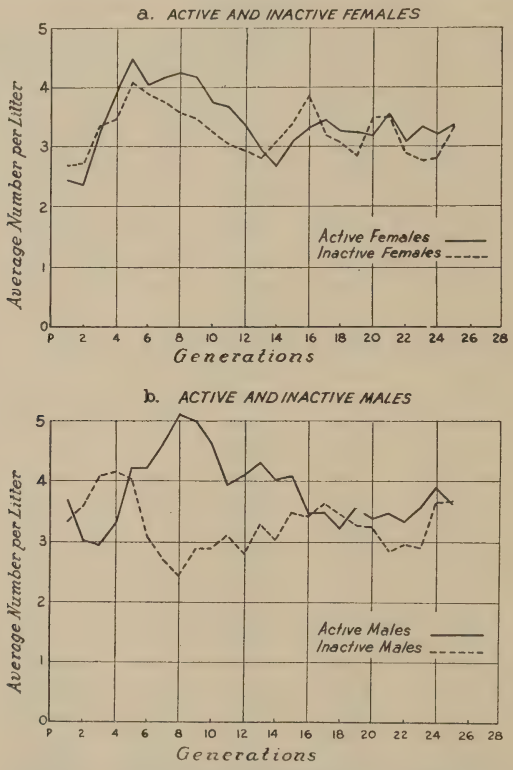

FIG. 6. SMOOTHED CURVES OF THE AVERAGE NUMBER OF MALES AND FEMALES PER LITTER IN THE ACTIVE AND INACTIVE STRAINS FROM THE F1–F25 GENERATION

B. *The effects of strain crosses on activity*[6]

This part of the investigation was undertaken after selective breeding had been in progress for twenty-one generations. Active females from the F_{21} generation were mated to F_{21} inactive males, and inactive strain females were mated to active males. The offspring from these crosses were subdivided into three comparable groups which were used in the following series of matings: (1) matings with each other to obtain the F_2 generation, (2) matings with animals from the inactive strain, and (3) matings with animals from the active strain. Similar crosses were made among active and inactive rats of the F_{22} generation.

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[6] The raw data for this section are on file with Dr. William T. Heron of the Psychology Department at the University of Minnesota.

The means and standard deviations of activity in the crossbred generations are presented in table 7. It will be noted that the mean activity in the comparable F_{21} and F_{22} crosses differs to a marked extent. Among both the males and females the activity of the F_1 generation derived from F_{22} crosses is considerably lower than in the F_1 generation derived from F_{21} crosses. However, the backcross and F_2 generations are more active in the F_{22} than in the F_{21} crossmatings. Although the mean of the F_2 generation is less than the mean of the F_1 generation in the first series of crosses and greater in the second series of crosses, in both groups of males and females the F_2 generation is intermediate in activity between the active and inactive backcrosses.

TABLE 7

The means and standard deviations of activity in the crossbred generations

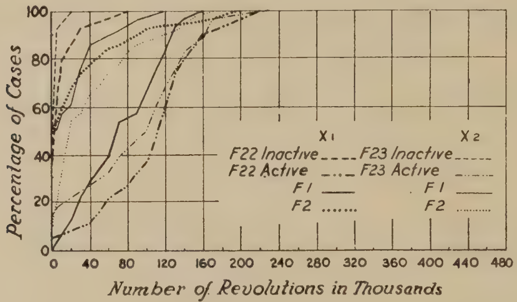
GENERATIONS	F_{21} CROSSES			F_{22} CROSSES		
	No. of cases	Mean	Standard deviation	No. of cases	Mean	Standard deviation
Females:						
F_1						
Active female parent	24	109,380	49,065	41	75,360	54,960
Inactive female parent	30	120,660	60,060	21	91,900	66,940
Total	54	116,115	56,250	62	80,960	59,800
Active backcross	42	128,580	69,280	23	182,180	43,200
Inactive backcross	22	40,900	66,600	23	52,600	52,200
F_2	99	68,780	66,000	30	142,500	79,750
Males:						
F_1						
Active female parent	7*	33,930	22,470	32	20,480	27,090
Inactive female parent	21	87,860	40,050	17	26,760	29,530
Total	28	74,640	43,100	49	22,350	27,900
Active backcross	45	55,340	57,200	26	94,620	61,200
Inactive backcross	20	2,350	3,740	14	11,317	12,804
F_2	96	32,700	44,000	35	42,000	46,920

* The small number of males in this cross is the result of an epidemic which eliminated three fourths of all the males at the age of one month.

In figure 7 the activity of the male and female offspring resulting from these crosses as well as the distributions of the F_{22} and F_{23} true strains are presented in the form of cumulative frequency distributions.

The cumulative curves are presented rather than frequency polygons for three principal reasons: (1) the distribution of several crosses can be shown on the same graph for comparison which would otherwise be impossible because of overlapping frequencies, (2) the range of frequencies is large in comparison with the number of cases and many intervals would contain zero frequencies unless the intervals were made so large that much of the variation would be obscured, and (3) the indication of the large proportion of very inactive rats in some of the distributions would necessitate using a scale in which the remaining frequencies would not be clearly represented. In addition, by this method it is possible to subdivide the inactive portion of the scale by plotting smaller and unequal intervals. Thus the percentages below one thousand, five thousand, and ten thousand revolutions are shown but thereafter all intervals are ten thousand revolutions in width.

1. *Fl and F2 Crossbred Males and the F22 and F23 Active and Inactive Strain Males*



2. *The Active and Inactive Backcross Males*

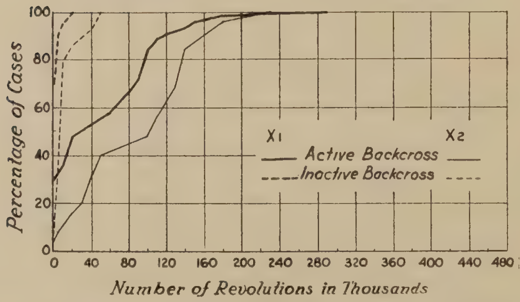


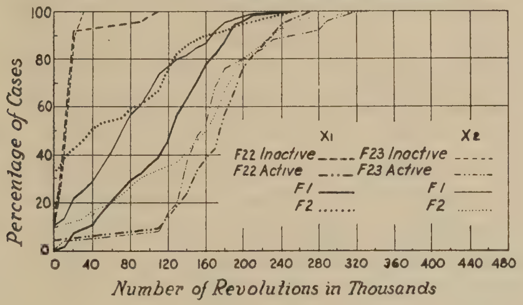
FIG. 7*a*. CUMULATIVE PERCENTAGE DISTRIBUTIONS OF THE ACTIVITY OF MALES DERIVED FROM CROSSES BETWEEN THE ACTIVE AND THE INACTIVE STRAINS

The offspring of the crosses between the F_{21} active and inactive strains are designated as X_1 whereas the offspring of comparable crosses between the F_{22} active and inactive generations are designated as X_2.

It will be noted that the two distributions of F_1 males (figures 7*a-1*) differ markedly in activity. The males from the F_{21} cross are only slightly less active than the active strain animals whereas the males from the comparable F_{22} cross approach the inactive strain in activity. Although 94% of the F_1 males in the X_2 crosses ran less than 80,000 revolutions, only 56% of the F_1 males in the X_1 cross ran less than this amount. The most marked difference between the X_1 and X_2 crosses is the percentage of very inactive rats. Fifty per cent of the offspring of the second cross but none of the first cross ran less than 1,000 revolutions.

The F_1 females from the F_{21} strain crosses are also more active than those from the F_{22} crosses (figure *7b-1*) but the difference is not as great as between the two distributions of males. Fifty-seven per cent of the X_2 females and thirty per cent of the X_1 females ran less than 80,000 revolutions; none of the X_1 females and eighteen per cent of the X_2 females ran less than 1,000 revolutions.

1. *Fl and F2 Crossbred Females and the F22 and F23 Active and Inactive Strain Females*



2. *The Active and Inactive Backcross Females*

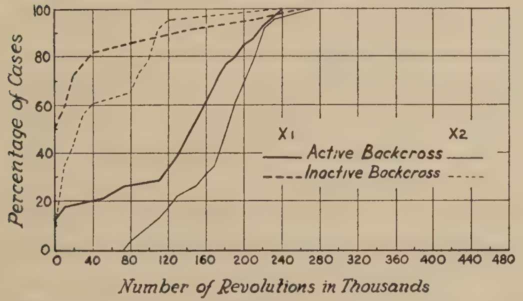


FIG. 7*b*. CUMULATIVE PERCENTAGE DISTRIBUTIONS OF THE ACTIVITY OF FEMALES DERIVED FROM CROSSES BETWEEN THE ACTIVE AND THE INACTIVE STRAINS

Both F_1 distributions of females are intermediate between the F_{22} and F_{23} active and inactive strains although the range of activity is approximately the same as for the active strain. Despite the fact that the F_1 animals derived from the F_{21} strain crosses were more active than those from the F_{22} crosses, the offspring of crosses involving the first F_1 generation are less active than the comparable crosses involving the second F_1 generation. The activity of the males and females in the F_2 generation and in both the active and inactive backcrosses is considerably greater in the X_2 than in the X_1 series of matings.

Although the percentage of animals included below any particular activity level differs in the comparable X_1 and X_2 crosses, it will be noted that the form of the distributions of activity among the males is remarkably similar in the two F_2 and backcross generations. The inactive backcross males (figure *7a-2*) are as inactive as the F_{22} and F_{23} true strain inactives. In neither the X_1 nor the X_2 cross did any of the inactive backcross males exceed 50,000 revolutions. The range of activity in the two generations of active backcross males (figure *7a-2*) is as great as within the active strain and it will be noted that the percentage of males above 100,000 revolutions is the same in the X_1 active backcross generation as in the F_{23} true active strain. Both of the active backcross generations are definitely bimodal, however, in contrast to the true strain actives, which indicates that segregation has occurred. The range of activity of the F_2 males (figure *7a-1*) also approximates that of the active strain. These distributions are intermediate between those of the backcross generations and the curves are smooth with no tendency toward bimodality. There are between twenty-five and thirty per cent more cases below 60,000 revolutions in the F_2 than in the corresponding active backcross generations.

Although the activity of the F_1 females in the X_1 and X_2 crosses differs less than the activity of the males, it is evident that the two groups of F_2 females (figure *7b-1*) differ far more in activity than the two groups of F_2 males. Above 90,000 revolutions, the distribution of activity among the first group of F_2 females is almost identical with that among the second group of F_1 females. On the other hand, the second F_2 females approximate the activity of the first F_1 females below 90,000 revolutions.

The females in the X_1 active backcross generation (Figure *7b-2*) are slightly less active than the females in the true strains but the X_2 active backcross females are more active than females in either the F_{22} or F_{23} active strains.

The females from the inactive backcrosses (figure *7b-2*), however, differ markedly from the true strain inactives since the range of activity is as great as within the active strain. The activity of the females in the F_{22} inactive backcross shows clear cut evidence of segregation similar to that shown by the active backcross males. Of interest is the fact that this distribution of females is practically identical with the distribution of activity among the males in the F_{21} active backcross. The activity of the F_{21} inactive backcross females, on the other hand, approximates the activity of second generation of F_2 males. It will be noted later in the analysis of the activity of females in the F_2 subcrosses that segregation may be obscured by factors which increase the number of very inactive offspring. This probably accounts for the absence of segregation in the activity of the F_{21} inactive backcross females.

The genetic differences between the two strains as indicated by the activity of animals derived from the various cross matings cannot be attributed to multiple factors. The inactive backcross males are as inactive as males from the true inactive strain and the active backcross females tend to be as active as females from the true active strain. These results as well as the clear cut segregation which occurs among both generations of active backcross males and the second generation of inactive backcross females support the hypothesis that a single gene pair is involved in which the inactive component is dominant in the males and recessive in the females. The effects of this gene, however, are evidently not invariable. The difference between the two groups of F_1 males illustrates the marked variation which can occur when the gene pair is in heterozygous condition. Undoubtedly a similar type of variation accounts for the fact that segregation is masked in some of the crosses but appears in others.

The number of cases in most of the generations is too small to permit a breakdown analysis into subclasses. However, several types of analysis were employed, where the number of cases permitted, in the attempt to isolate some of the sources of variation.

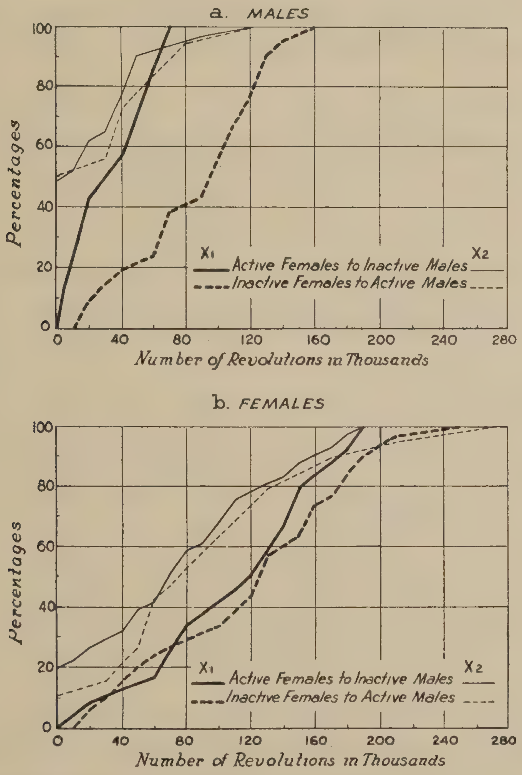


FIG. 8. CUMULATIVE FREQUENCY DISTRIBUTIONS OF THE ACTIVITY OF F1 MALES AND FEMALES FROM RECIPROCAL CROSSES AMONG BOTH THE F21 AND F22 ACTIVE AND INACTIVE STRAINS

In figure 8 the F_1 distribution of both the F_{21} and F_{22} crosses of inactive females to active males and active females to inactive males are presented separately. It will be noted that the distributions of the activity of females in the reciprocal crosses are very similar (figure 8*b*) but that both groups are lower in the F_{21} than in the F_{22} crosses. Since the distributions of reciprocal crosses are much more alike than those of comparable crosses, random errors are evidently of far less importance than environmental factors in determining differences among crosses.

The distributions of activity for the males from the reciprocal F_{22} crosses are also almost identical (figure 8*a*) but the difference between the reciprocal F_{21} crosses is very marked. The number of males in these reciprocal crosses also differs markedly. Although about the same number of males were produced by both types of mating, at the age of about one month all but seven of the males from the cross of active females to inactive males died. If it were not for this epidemic it is probable that the animals in this subcross would not have differed significantly from those in the reciprocal cross in view of the similarity in activity between the F_{22} reciprocal crosses. The similarity between the X_1 and X_2 reciprocal crosses for the females and between the reciprocal crosses of X_2 males is further evidence that only a single gene pair differentiates the two strains; with more than a single gene pair the crosses would be expected to differ considerably as a result of sampling errors alone.

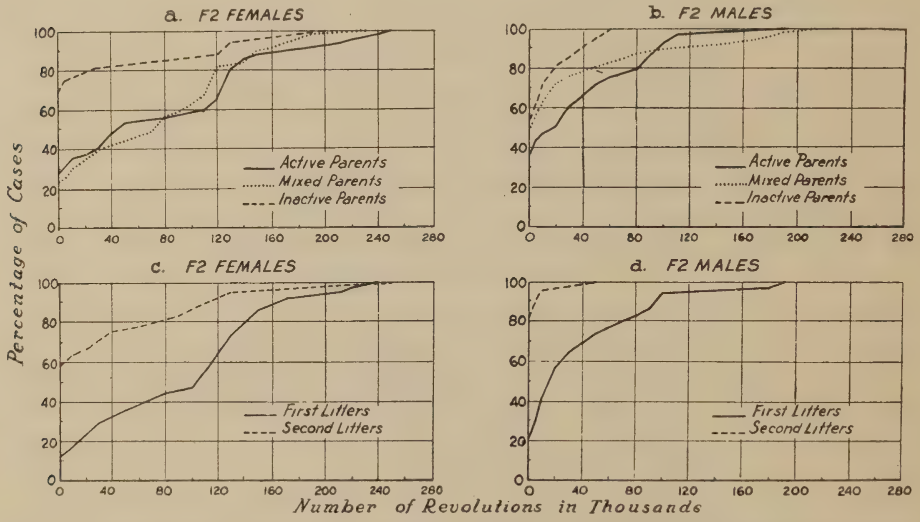


FIG. 9. CUMULATIVE FREQUENCY DISTRIBUTIONS OF THE ACTIVITY OF OFFSPRING FROM SUBCROSSES AMONG THE F1 GENERATION RATS DERIVED FROM THE F21 ACTIVE AND INACTIVE STRAINS

In matings between the two pure strains all individuals in the F_1 generation would be expected to have the same genetic constitution. To determine the extent of genetic similarity among the F_1 animals derived from crosses between the F_{21} active and inactive strain, matings among the F_1 rats were subdivided into three classes: (1) both parents above 100,000 revolutions, (2) both parents below 70,000 revolutions, and (3) one parent above 100,000 and one below 70,000.

The differences among the offspring of these classes are shown in figure 9. The three types of mating are clearly differentiated in the distributions of the F_2 males (figure 9*b*). The crossing of phenotypically inactive rats produced no very active males, and a larger proportion of very inactive males were produced than in the crosses of phenotypically active rats. The females from the active and the mixed crosses are almost identical in activity in contrast to the males (figure 9*a*), but the inactive cross females are markedly lower in activity.

Although these differences among the F_2 offspring suggest genetic heterogeneity within the F_1 generation, the only differences in female activity consist of the larger proportion of animals below 1,000 revolutions from phenotypically inactive matings.

The final comparison among F_2 offspring is that between the first and second litters obtained from twelve pairs of F_1 rats in which both active and inactive animals were represented. Approximately one month after the first litters were born, the same males and females were remated. The distribution of the activity of offspring from these duplicate matings are shown in figures 9*c* and 9*d*. That both the males and females in the second litters were markedly lower in activity is apparent. No very active males resulted from the second matings, but the range of activity is the same for both the first and second litters of females.

The difference in activity between F_2 females from active and inactive F_1 parents and between the first and second litters is due exclusively to the different proportions of animals below 1,000 revolutions. If the proportions of females at different activity levels are recalculated with the very inactive animals omitted, the distribution of animals from the second set of litters is almost identical with those from the first set of litters, and the females from inactive parents are identical with those from active parents. It is evident that this is not true of the males since in both cases the most active males have been completely eliminated.

The differences between the first and second litters illustrate the marked susceptibility of activity to environmental influences. These differences could be the result of either one of two factors: (1) environmental differences at the time the animals were run in the activity cages, or (2) environmental differences during development such as physiological changes within the female parent during pregnancy. That the latter factor is probably responsible for the variation is indicated by the fact that the activity of other animals placed in the activity cages at the same time was not correspondingly depressed. In addition, if the former factor were involved the animals would be expected to vary during the fifteen-day period rather than to maintain their extreme inactivity uniformly throughout the testing period. That the difference between the offspring of active and inactive parents is also probably attributable to environmental factors is suggested by the fact that the distributions of activity among the females do not differ significantly if the very inactive rats are omitted.

The most significant source of variation in the comparable X_1 and X_2 generations of crossbred animals consists of the differing proportions of very inactive rats. The percentages of animals that ran less than 1,000 revolutions throughout selection were previously presented. In table 8 the proportions included below this amount are shown for the various crosses, and in comparison the mean, the minimum, and the maximum percentages found within the true strains are also presented.

In the first F_1 cross no very inactive animals occurred, but in all the crosses of these rats with each other or with either of the true strains a considerable number ran less than one thousand revolutions. It will be noted that the proportion is largest in the inactive backcross, least in the active backcross, and that the F_2 is almost exactly intermediate between the two backcross generations. In the second F_1 cross a large proportion of rats were also very inactive. The results from the reciprocal matings are presented separately to determine whether the offspring from the inactive females were more likely to be inactive than those from the active females. The differences among the males are certainly insignificant and among the females the active female parent had a larger proportion of very inactive offspring. Only a small number of rats ran less than one thousand revolutions in the crosses involving these F_1 animals and what differences there are show the largest proportion occurring in the F_2 generation. It will be also noted that the sex difference in these crosses is small and inconsistent in contrast to the much larger proportion of inactive males than females in the first group of cross matings and in both the true strains.

TABLE 8

Percentage of very inactive rats obtained in the crossbred generations

	FEMALES	MALES
All active generations:		
Average	0.8	2.6
Minimum	0.0	0.0
Maximum	6.5	14.3
All inactive generations:		
Average	8.5	24.1
Minimum	0.0	0.0
Maximum	26.1	50.0
F_{21} crosses:		
Active females to inactive males	0.0	0.0
Inactive females to active males	0.0	0.0
Total F_1	0.0	0.0
F_1 active backcross	12.8	28.6
F_1 inactive backcross	50.0	70.0
F_2	32.3	45.3
F_{22} crosses:		
Active females to inactive males	19.5	48.4
Inactive females to active males	10.5	50.0
Total F_1	16.7	49.0
F_1 active backcross	0.0	4.0
F_1 inactive backcross	8.7	5.0
F_2	10.0	11.4

As previously noted the number of very inactive rats did not increase despite rigorous selection and the activity of the offspring from matings of very inactive animals to each other did not differ significantly from the activity of inactive strain animals obtained from less inactive parents. However, in the first F_1 series of crosses, the percentage of very inactive rats varies in direct proportion to the proportion of inactive strain animals entering into the crosses. Although this would appear to indicate a genetic basis for extreme inactivity, it seems more likely that environmental factors which affect the entire distribution are involved. If the general level of activity were lower by a constant amount for animals in all the crosses involving the first F_1 generation the effect upon the inactive extreme would be differential in accordance with differences in the basic gene pair.

CONCLUSIONS

Selective breeding has had no effect upon increasing the mean activity or reducing the variability within the active strain. Although the generations differ significantly from each other, the differences are evidently attributable primarily to environmental rather than to genetic variation.

Strain separation occurred suddenly in the fifth generation through the elimination of active offspring from the matings among phenotypically inactive rats. From this time on the proportions of active animals within the inactive strain decreased to some extent which indicates that the inactive strain at the time of initial separation was partially heterozygous for modifying factors involved in activity. However, the form of the inactive distributions did not change as a result of selection. Furthermore, the proportions of very inactive rats did not increase which would be expected if an increased homozygosity of independently segregating primary genes were involved. This suggests that the decreased number of active deviates within the inactive strain resulted from a general decrease in heterozygosity attributable to inbreeding rather than to an increase in specific factors for inactivity. The tendency for litter size to decrease concomitantly supports this hypothesis.

That the two strains differ with respect to a single gene rather than with respect to multiple factors is indicated by the results of cross matings between the F_{21} and F_{22} generations. The gene apparently behaves as a dominant in the males and as a recessive in the females. This is indicated by the fact that the inactive backcross males are as inactive as the inactive strain and that the active backcross females tend to be as active as the active true strain females. Environmental factors evidently obscure the segregation in some of the crosses, but it is clearly present in the distributions of active backcross males and in the first cross of inactive backcross females.

Although environmental influences operative at the time the animals are placed in the activity cages may affect activity, the tendency for the distance traveled per day to remain relatively constant suggests that the effects of the environment are irreversible. The physiological condition of the female during pregnancy evidently is such a factor, for it has a marked effect upon the number of animals that are very inactive.

It has generally been assumed that individual differences in quantitative characters can be attributed to the independent assortment and segregation of genes as are differences in qualitative characters but that a larger number of gene pairs cumulative in effect are involved. This multiple factor hypothesis seems to account adequately for the results obtained from many selective breeding experiments. In case of activity, however, the difference between strains results from a single gene pair. The gene which determines inactivity must act as an inhibitor since none of the matings within the inactive strain produce active offspring, but, on the other hand, active strain matings produce individuals which vary from extreme inactivity to extreme activity. The effects of this gene are not invariable, however, but regulate activity only within certain limits.

Although the variation which is expressed phenotypically cannot be explained in terms of any theory involving the combination of discrete events, it is probable that some of the variability within both strains depends upon multiple factors which act as modifiers but are not specifically involved in activity. It is suggested that within the limits prescribed by the basic gene pair, differences in activity are in part the result of variations in the genic pattern but that the factors involved in this pattern are similar in both the active and inactive strains. A number of other quantitative traits may behave similarly in that the basic expression of the trait is determined by one or two genes but the final expression in the individual is conditioned by many interdependent factors both genetic and environmental in origin.

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